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Connection of Insects with the Soil in Different Climatic Zones*)

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In my communications at the X-th International Congress of Entomology (1956), at the XIV-th International Congress of Zoology (1958) and in my previous communications (c. f. Ghilarov, 1949). I stressed that the habit of dwelling in soil should be regarded as in many respects intermediate between aquatic and terrestrial life in the open atmosphere. The air in the soil is saturated with water vapour permitting air breathing without the danger of desiccation. I have drawn the conclusion that in many groups of invertebrates the transition from aquatic to terrestrial life in the course of the phylogenesis has proceeded through the soil.

Actually, representatives of many aquatic invertebrate groups when leaving their native water habitats become mainly soil dwellers or inhabitants of allied substrates. And, conversely the inferior representatives of terrestrial animal groups which have still not acquired the ability to resist desiccation are soil dwellers also.

The humidity of the air in the soil at some depth being at saturation level even in arid localities, representatives of various hygrophilous animal groups are to be found there, being typical soil inhabitants (woodlice, millipedes, centipedes, Onychophora, Onychiurids, Diplura etc.).

Pterygote insects are regarded as the invertebrates most fitted to life in the open air, in conditions of humidity deficit. Adaptations to saturation deficit in the surrounding air are especially evident in adult Pterygota, as the larval stage of the majority of holometabolous insects is connected with soil or other shelter where the high humidity preserves soft skinned larvae from desiccation. But even the adult stage in different kinds of Pterygota is resistant to different extents to the deficit of moisture in the atmosphere. Therefore with lowering of the air humidity many insects change over to the life in the soil and similar sheltered places.

For example the plant louse *Xerophilaphis scorzonerae* Mordv. in the dry period inhabits roots of Compositae-Liguliflorae but after heavy rains occurs on their leaves (Ghilarov, 1937). Species with a range embracing different climatic zones, which in the humid zones inhabit the above-ground parts of plants, change over in the arid zones to subterranean life. Bark-beetles *Blastophagus piniperda* L., *Neotomicus laricis* F. and *Hylurgops palliatus* Gyll. may serve as demonstrative examples. These species, inhabiting twigs or trunks of trees in the forest zone, attack roots at a considerable depth down to 100 cm in the afforested area in semi-desert Transvolga region. Many Cercopids and Membracids develop on leaves of their food-plants in humid valleys on river banks but in the drier conditions of mountain slopes become root suckers. The larvae of the stag-beetle *Lucanus cervus* L. develop in the zone of deciduous forests in rotten tree stumps but in the forests planted in the steppe zone (Rostov region) are to be found in decaying roots of trees at a depth 60—80 cm (Ghilarov, 1959).

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In such insect groups which are very succeptible to drying up and are associated with the soil stratum, the degree of such an association differs among various representatives inhabiting different localities. E. g. the termites do not experience an unsaturated atmosphere and air movement being closely connected with soil. In localities with periodically occuring heavy rainfall the termites build their subconical or mushroom-like hills, widely known as termitaria on the soil surface. Under such protection the termites enjoy permanently saturated air, avoiding contact with water droplets, which are as dangerous for these soft-skinned insects as evaporation. In the shade of tropical rain forests the air humidity reaches saturation point and in these conditions many termites construct suspended nests on trees, serving rather as roofs only, since enclosed shelters are not so necessary in moist air. On the other hand, in dry deserts of Kara-Kum, Sakhara and S. Africa the termites (family Hodotermitidae) are strictly underground dwellers, having their nests at a depth down to 12 metres. Analogous conditions are to be observed when we compare the buildings of ants gen. *Formica* in different zones.

The Tenebrionids in wetter zones (in forests) develop in decaying timber of tree stumps and logs, whereas in arid zones (in steppes and deserts) the numerous representatives of this species-rich family are soil dwellers not only in the larval stage but often in the adult stage as well. The longicorn beetles of the genus *Prionus* may serve as another example. In our deciduous forests *Prionus coriarius* L. inhabits decaying tree-stumps, but related species (*P. brachypterus* Gebl., *P. turkestanicus* Sem.) in the deserts of Central Asia are soil dwellers feeding on roots of herbacious plants.

There is no need to multiply the number of such examples: insects insufficiently protected against desiccation in zones of moderate humidity live near the soil surface, in humid zones become the inhabitants of above-soil parts of plants whereas in arid zones they develop in the soil, being strict soil dwellers.

This "Rule of the Zonal Change of Strata" (Ghilarov, 1951) is very closely related to the "Rule of the Zonal Change of Stations" formulated by G. Bey-Bienko (1958).

The present author and his assistants have studied the soil fauna in different climatic zones from the tundra to the deserts of Central Asia and to the subtropical forests of the Transcaucasia in order to reveal the general distribution patterns of insects and other invertebrates in the soil. The zonal soil types under undisturbed natural vegetation (in native forests and steppes in National Parks) were investigated. The general results of this 15 year investigation are as follows.

In the moss tundra the activity of a rather scarce soil invertebrate population is restricted to the very surface of the soil and even the representatives of such insect groups which are common soil dwellers are active not in the soil but between the moss plants (wireworms *Sericus brunneus* L., Collembolans *Onychiurus armatus* Tullb. etc. may serve as typical examples). Correspondingly the soil cover in tundra is but feebly developed.

In the zone of taiga, in coniferous forests soil animals are active in the litter and in a very thin adjacent superficial soil horizon. This corresponds to the virtual absence of the accumulative humus horizon (A_1) in true podzols — soil type which is intrinsic to the taiga. The predominating groups among the insects in the taiga soils are different hygrophilous larvae of Nematocera: Tipulids, Limoniids, Heleids, Chironomids, Bibionids etc. Of the beetle larvae Elaterids are most widely distributed, all species being connected with raw humus (*Eanus costalis* Payk., *Orithales serraticornis* Payk., *Athous subfuscus* Müll. etc.). Due to the small quantity of soil animals and short period of their activity the decomposition of the litter in the taiga occurs without mechanical destruction of plant tissues (mor type). The soil is wet throughout the summer in the taiga, therefore bad aeration prevents penetration of insects into deeper horizons. Therefore the organic matter cannot be transported from the surface into deeper soil layers otherwise than in dissolved form;

subsequently leaching of soluble nutrients occurs and the leached podzolized A_2 horizon is formed, whereas the formation of the A_1 horizon is inhibited.

Semi-podzol soils (now often called "dern-podzol soils") are characteristic of the zone of mixed forests. In these soils the accumulative humus horizon A_1 is already present reaching ca. 10 cm, or sometimes even 25 cm in the southern regions of the zone. During the summer the upper layers of the soils in mixed forests are not as wet as in spruce forest of the typical taiga, the soil aeration is better, enabling soil animals to migrate and be active in the soil down to the depth corresponding to that of the humus horizon. Of the bigger soil insects Diptera, both Orthorrhapha and Nematocera (but only moderately hygrophilous ones, such as Bibionids, Tipulids etc.) and Coleoptera [mostly Elaterids (*Athous subfuscus* MÜLL., *A. haemorrhoidalis* F., *Corymbites* spp.)] prevail. In the summer the transportation of organic matter from the soil surface into the soil in the intestines of invertebrates results in the formation of the A_1 horizon in semipodsols.

In the still drier conditions in the zone of deciduous broad leaved forests, mainly oak forests in this country, so called grey forest soils are formed under the forest floor. The accumulative humus layer (A_1) of these soils is better developed, reaching up to 40 cm. The coloration of this layer is almost black in the moist, but grey in the dry condition. The warm period in these zone is longer and in summer time the soil becomes drier enabling insects and other animals to penetrate down to the depth ca. 40 cm without ceasing their activity, as in the upper horizon of the soil both aeration and water supply are favourable for the activity of soil dwellers throughout the warm period. Among the larger insects in these soils Coleoptera represent the predominant group. Not only wireworms, especially *Athous haemorrhoidalis* F., *Dolopius marginatus* L., *Selatosomus aeneus* F., *S. globicollis* GERM. etc.), but also many other families (Scarabaeidae, Tenebrionidae, Alleculidae, Curculionidae) become abundant. Of Diptera the Orthorrhapha are rather numerous, the Nematocera being a relatively insignificant group.

Further southwards in the steppe zone under the rich herbaceous steppe vegetation black soils — chernozems are formed. These are well developed soils with a thick accumulative humus A_1 horizon which sometimes reaches up to 120 cm almost without any change in coloration, being black not only when moist but also when dry.

In steppe chernozems the larvae of insects and other soil animals in the wet period are active near the surface; when the soil becomes drier its population migrates deeper and deeper, some components without interrupting their activity, because the rootlets in this soil penetrate to deep horizons, the humus content is high and aeration of the soil consisting of crumbs is so good that it permits animal activity even at the border line of parental loess. E. g. in thick chernozem near Kursk active weevil-larvae and other larval insects were permanently encountered in midsummer at the depth 120 cm (ARNOLDI und GHILAROV, 1963). The overwhelming majority of larger soil insects in chernozems are beetle larvae — Scarabaeids Omophlinae, Elateridae (mainly *Agriotes gurgistanus* FALD. and *Selatosomus latus* F.), various Tenebrionidae, *Dorcadion* spp. of Longicorns, different Curculionids, etc.

Diptera are not numerous, Asilids are common. Soil invertebrates are the main factor of plant matter transportation from the surface into the deep soil. They are tunnelling the soil, maintaining its non-capillary porosity and so creating the crumb-like texture, typical of a chernozem, on which its perfect drainage and aeration depend.

In the steppe zone the interdependence between the depth of downward migration of soil animals and the depth of the humus layer is very evident. In those spaces, where the invertebrate penetration into soil is prevented not by excessive moisture and lack of aeration, but e. g. where the deeper horizons are rich in easily soluble salts, in solonets soils the humus horizon is thin, as in the podzolized soil coinciding with the depth of possible vertical migration of animals, unable to withstand the high salinity of the medium.

Still further to the south-east in Central Asian deserts the total population density of soil insects is much lower than in chernozems, whereas the depth of their penetration increases. Due to the sparse vegetation in deserts and to the relatively small number of soil dwellers and the short period of their activity (in hot summer months the majority of soil insects is in inactive state), the desert soils are poor in humus, though the vertical distribution of organic matter in the soil is very great — down to 200 cm even in clay soils. This is characteristic of desert gray soils, called "sierozems". Since the transportation of organic matter occurs through the participation of soil animals, mainly insects, it is clear that soil dwelling insects (larvae of *Pleonomus*, of *Prionus* etc.) are to be found in summer at a depth ca. 2 m, mostly in an inactive state. In deserts not only larvae but also adults of many insects are characterized by their hidden mode of life, especially during the daytime, living in the soil or in its cavities (cracks, vertebrate burrows etc.).

Contrarywise, in wet subtropical regions of the Blacksea coast of the Transcaucasia, red soils ("krasnoziems") and podzolized red soils are formed. The profile of such soils has much in common with podzolic ones, their humus horizon does not exceed 15 cm, the deeper layers being significantly leached. The distribution of insects and other soil animals in red soils is also connected with this upper layer.

In this connection it is of interest to consider the soils of tropical rain forests. In tropical rain forests the air under the tree cover is saturated with moisture; therefore in these forests there is no true soil fauna — in some respects there is an analogy with tundra. Animals do not occur beneath the litter whilst, on the other hand many eudaphic species are dwellers on trunks and twigs of trees, where even so called suspended soils are formed ("sols suspendus" of Delamare Debouteville, 1951). These suspended soils forming on trees are inhabited by many representatives of soil insects, as Onychiurids etc.

The connection between the distribution of the humus through the soil profile and the depth of insect and other animal migration in the soil is not a fortuitous one. The accumulation of the humus in the soil depends on the distribution of root-systems of plants and on the depth down to which animals can bring plant debris from the surface; the humification of plant remains proceeds with the participation of soil invertebrates also. The distribution of plant roots is connected with the thickness of the humus layer (plants consume nutrients released in the course of humus mineralization) whereas the penetration of rootlets deep into the soil is facilitated by channels bored by soil dwelling insects and other animals. The limits of the penetration of invertebrates into the soil are connected with boundaries of root distribution (in the case of phytophagi) and with those of the humus horizon (for saprophagi).

The depth of downward migration of animals in the soil is always limited by the depth of the sufficient aeration. But on the other hand, the digging activity of animals contributes to the deepening of the humus layer; this is to be observed in deep sections through the soil and subsoil strata. Some passage-ways made by animals and filled with humus-containing matter from the upper layers can be found in the subsoil deeper than the humus horizon. In this way the natural deepening of the soil stratum proceeds. But such deepening does not continue indefinitely. Pores, cavities and passage-ways formed as a result of the digging activity of soil insects and other animals may become permanently destroyed or filled with solid particles due to the penetration of rain water, to the influence of the gravity etc.

As a result of this the porosity of the soil decreases, its drainage and aeration become worse and subsequently soil animals must move nearer to the surface. As animals now leave deep horizons and their activity, maintaning soil porosity in the deep layers ceases, they disappear and do not return until the restoration of drainage in the upper layers. So a permanent rise of porosity due to the animal activity takes place in the soil as well as permanent destruction of pores due to water, gravity etc. (Ghilarov, 1947).

The level of the intensity of the digging activity of soil animals determines the depth of the accumulative humus horizon, being reciprocally determined by this in turn. This depth, corresponding to the depth of insect penetration into the soil, is different in different zones depending on the hydrothermal regime which influences the water supply and aeration of the soil.

So interrelationships of insects and soil in different zones conform to a predictable pattern.

Summary

The degree of connection of insects with the soil depends on the climatic conditions of the given locality, on the hydrothermal regime of the soil. In humid zones the percentage of insects developing in the soil is less than in arid ones. The depth of penetration by insects and other invertebrates into the soil determines to a great extent the development of the accumulative humus layer of the soil. The depth of penetration into the soil of active saprophagous animals depends on the depth of the humus layer of the soil. Consequently the depth of the humus layer of the soil and the depth of downward migration of insects into the soil are reciprocally connected.

Zusammenfassung

Der Grad der Bindung an den Boden hängt bei Insekten von den klimatischen Bedingungen der gegebenen Örtlichkeit ab, die das hydrothermale Regime des Bodens bestimmen. In humiden Zonen ist der Prozentsatz der sich im Boden entwickelnden Insekten geringer als in ariden. Die Eindringtiefe von Insekten und anderen Wirbellosen bestimmt in hohem Maße die Entwicklung einer akkumulativen Humusschicht des Bodens. Gleichzeitig hängt aber auch die Durchdringung des Bodens durch aktive saprophage Tiere von der Tiefe der Humusschicht ab. Folglich sind die Tiefe der Humuschicht des Bodens und die Tiefenwanderung von Insekten reziprok bedingt.

Резюме

Степень связи насекомых с почвой зависит от климатических условий местности, определяющих гидротермический режим почв. Во влажных местностях процент развивающихся в почве насекомых значительно меньше, чем в сухих. Глубина проникновения в почву насекомых и других беспозвоночных в значительной мере определяет мощность гумусового горизонта почвы. В то же время возможность проникновения вглубь активных почвенных сапрофагов зависит от мощности гумусового горизонта, т. е. степень развития аккумулятивного слоя почвы и глубина миграций почвенных насекомых и других беспозвоночных — величины взаимно друг друга определяющие.

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